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PALAEOMYIA BURMITIS (DIPTERA: PHLEBOTOMIDAE), A NEW GENUS AND SPECIES OF CRETACEOUS SAND FLIES WITH EVIDENCE OF BLOOD-SUCKING HABITS

GEORGE POINAR, JR.

Department of Zoology, Oregon State University, Corvallis, OR 97331, U.S.A. (e-mail: poinarg@casco.net)

Abstract.—***Palaeomyia burmitis*** **Poinar** (Phlebotomidae: Diptera), a **new genus** and **new species** of sand flies, is described from Cretaceous Burmese amber. This genus and species differs from extinct and extant members of the family by the following combination of characters: small size (under 1 mm); 18—segmented antennae; Rs shorter than R_{2-4}; R_1 longer than R_{2+3}, R_{2-4} longer than R_{2+3}; discal cell open basally; vein R_2 shorter than R_{2+3} obliquely reaching costal margin; basal part of M_3 separated by a short crossvein from M_{1+2}; vein CuA_2 short; and anal vein absent. The presence of a well-developed proboscis with piercing type mandibles and maxillae and a blood meal in its midgut indicates that this specimen was a blood feeder. *Palaeomyia burmitis* is considered a progenitor of the *Sergentomyia* clade, an Old World genus that feeds on reptiles.

Key Words: *Palaeomyia, Palaeomyia burmitis,* Phlebotomidae, Burmese amber, Cretaceous

The moth flies (Psychodidae) and sand flies (Phlebotomidae) are closely related primitive Diptera that are often treated as subfamilies in the family Psychodidae (Quate and Vockeroth 1981). The fossil record of sand flies has been summarized by Evenhuis (1994) and consists mostly of Tertiary forms (Meunier 1905, Stuckenberg 1975). The oldest sand flies, comprising several extinct genera, have been described from Lower Cretaceous Lebanese amber (Hennig 1972, Azar et al. 1999).

A female sand fly from Lower Cretaceous Burmese amber is described below in a new genus and compared with extinct and extant phlebotomids. Based on the structure of the mouthparts and remains of a blood meal in its gut, the fossil fly apparently fed on vertebrate blood shortly before its entombment in resin.

MATERIALS AND METHODS

The amber was recut and polished in order to better view the specimen. The amber piece containing the fossil is square in outline, measuring 5 mm along all sides and 2 mm in width. The specimen is well preserved and nearly complete. The middle left leg and the tips of the tarsi on both hind legs are missing, and there is a small circular opening in the pleura of the sixth abdominal segment, possibly made by a predator, since the gonads are missing. Observations, drawings and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope (with magnifications up to 650×). Amber from Burma (Myanmar) occurs in lignitic seams in sandstone-limestone deposits in the Hukawng Valley. These lignitic seams extend from the valley up the sides of a mountain where the mine that contained this specimen is located (Jim Davis, personal communication). Nuclear magnetic resonance (NMR) spectra of amber samples taken from the same locality as the fossil indicated an araucarian (possibly *Agathis*) plant source (Lambert and Wu, personal communication). Palynomorphs obtained from the amber beds where the fossil piece originated have been assigned to the Upper Albian (~110–100 mya) (Cruickshank and Ko 2003). While an Eocene age was originally provided for these deposits (Chhibber 1934), Cockerell (1922) was the first to suggest they were Cretaceous based on primitive insect types found in the amber, and others have concurred (Zherikhin and Ross 2000). Terminology in the description follows that presented in the "Manual of Nearctic Diptera" (McAlpine 1981).

Family Phlebotomidae Kertész 1903
Subfamily Phlebotominae Kertész 1903

Palaeomyia Poinar, new genus

Description.—Small size (under 1 mm); eye bridge absent; 18—segmented antennae; flagellomeres fusiform (Fig. 1); palp with five palpomeres, terminal one longest, second segment shorter than fourth (Fig. 3); wing (Fig. 2) with Sc not reaching costa; Rs shorter than R_{2-4}; R_1 longer than R_{2+3}; R_1 meeting costa at middle of wing; R_{2-4} longer than R_{2+3}; discal cell open basally; vein R_2 shorter than R_{2+3}, obliquely reaching costal margin; basal part of M_3 separated by a short crossvein from M_{1+2}, so that CuA_1 and medial veins appear to arise from CuA_2; vein CuA_2 short; anal vein absent.

Etymology.—"Palaeo" is from the Greek "palaios" for ancient or old (masculine); "myia" is from the Greek "myia" for fly (neuter).

Diagnosis.—The absence of an eye bridge, fusiform flagellomeres, Rs four branched, 2 longitudinal veins present between the radial and medial forks, and A_1 absent, place the fossil in the Phlebotomidae (Lewis 1973; Quate and Vockeroth 1981).

Type species.—*Palaeomyia burmitis*, n. sp.

Palaeomyia burmitis Poinar, new species
(Figs. 1–6)

Description.—Characters as listed under generic description. Very small species with a body length of only 0.887 mm; body light brown; legs and antenna dark brown.
Head length, 0.146 mm; length of proboscis, 0.144 mm; length of maxillary palp, 0.236 mm (Fig. 3), extending beyond tip of proboscis, fifth palpal segment longest, first shortest, closely associated with second; relative lengths of palpal segments, 1, 0.04; 2, 0.12; 3, 0.27; 4, 0.19; 5, 0.37; antenna (Fig. 1) with scape short, stout, pedicel globular, 16 fusiform flagellomeres, becoming shorter at apex, flagellomeres bearing scales and variously sized setae; ascoids absent or obscured by setae and scales.

Thorax with well-developed mesoscutum; mesoscutellum greatly reduced; postscutellum large, convex; wing length, 0.945 mm, membrane hyaline, covered with minute granules, microtrichae absent; humeral vein perpendicular to costa, wing (Fig. 2) with Rs four-branched, with all branches extending to wing margin; R_3 and R_4 curved anteriorly at costa; R_5 straight; veins M_1 and M_2 straight, nearly same length; basal part of M_3 separated by a short cross vein from M_{1+2}; vein CuA_2 short; main veins and wing margin with macrotrichiae; longer setae occur along posterior wing margin, especially in anal area; length of halter, 0.117 mm; legs long, bearing numerous setae and scales; femora longer than corresponding tibiae, tarsi 5-segmented with first segment longest, nearly equal to remaining segments, terminal segment shortest; tarsal claws simple, small, paired, surrounded by hairs, some with apparent secretions at tips (Fig. 5); spermatheca and associated reproductive structures missing; cibarium not visible.

Abdomen extended, seven segments

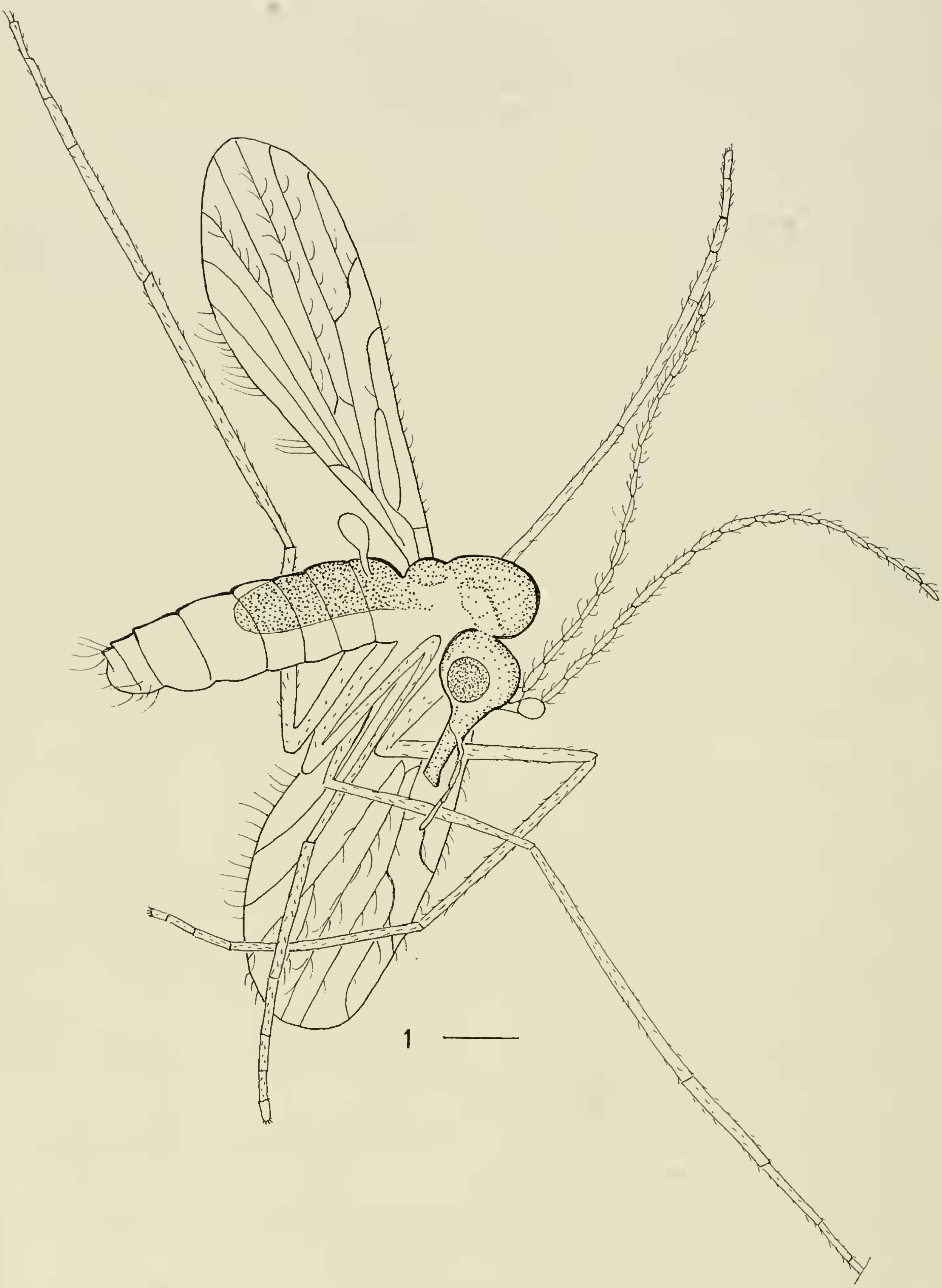
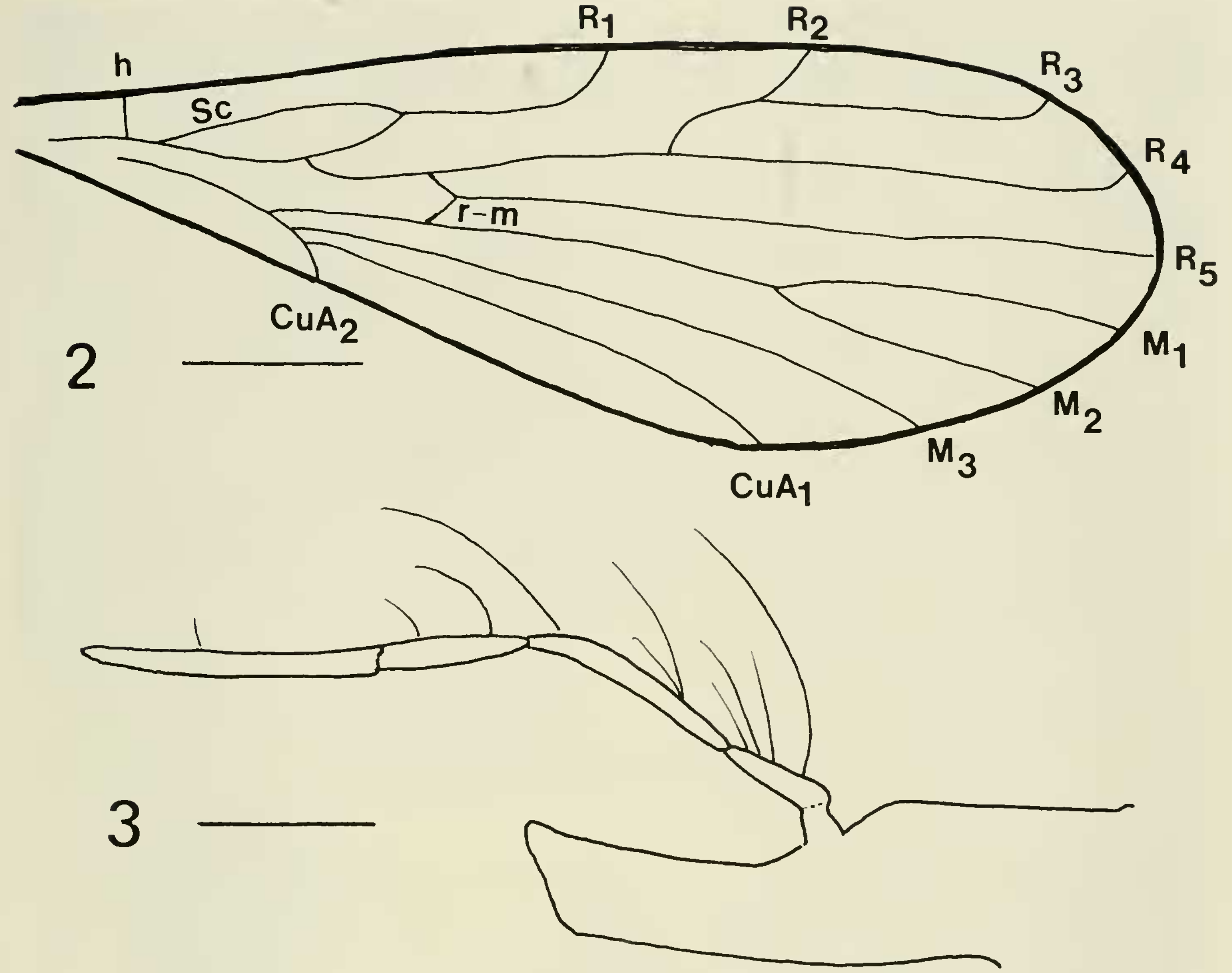


Fig. 1. *Palaeomyia burmitis* in Burmese amber. Dark stippled area in gut represents blood meal. Bar = 140 μm.



Figs. 2–3. *Palaeomyia burmitis* in Burmese amber. 2, Wing showing veins referred to in this study. Setae are omitted. Bar = 140 μm. 3, Five-segmented maxillary palp. Bar = 45 μm.

clearly visible (Fig. 1); length, 0.548 mm; with remains of blood meal in midgut.

Male.—Unknown.

Material examined.—Holotype female in Burmese amber deposited in the Poinar amber collection (accession # B-D-16) maintained at Oregon State University. From lignitic seams in sandstone-limestone deposits in the Hukawng Valley, Burma (Myanmar).

Etymology.—From "Burma" referring to the country where the fossil originated.

Comments.—The cluster of hairs, many of which bear apparent terminal secretion drops, at the tips of the terminal tarsal segments is curious. These might be considered retineriae (hollow hairs through which a viscous substance is secreted) (McAlpine 1981) and could have played a role in anchoring the sand fly to the substrate or host during a blood meal. The long fifth palpal segment is a character found in Old World sand flies and separates them from New World forms (Lewis 1973).

Diagnosis.—The only previous description of a phlebotomid from Burmese amber is *Eophlebotomus connectens* Cockerell (1920), which was recently redescribed and re-evaluated by Duckhouse (2000). The presence of only 13 flagellomeres, palpal segments 4 and 5 short and subequal, Sc with a costal branch and M_3 and CuA_1 fused at the base to form a pedicel, separate *E. connectens* from *P. burmitis.*

Palaeomyia burmitis has some features of the early Cretaceous Lebanese *Phlebotomites brevifilis* Hennig and *P. longifilis* Hennig (Hennig 1972). However, in both of these species, the termination of R_1 is distal to the fork of R_{2+3} and R_4 while the termination of R_1 is proximal to this fork in *P. burmitis*. Also, both *Phlebotomites* species have branch R_{2+3} longer than R_{2-4} while R_{2+3} is shorter than R_{2-4} in *P. burmitis*. In addition, in *P. brevifilis*, the third palpal segment is the longest, not the terminal one as in *P. burmitis*.

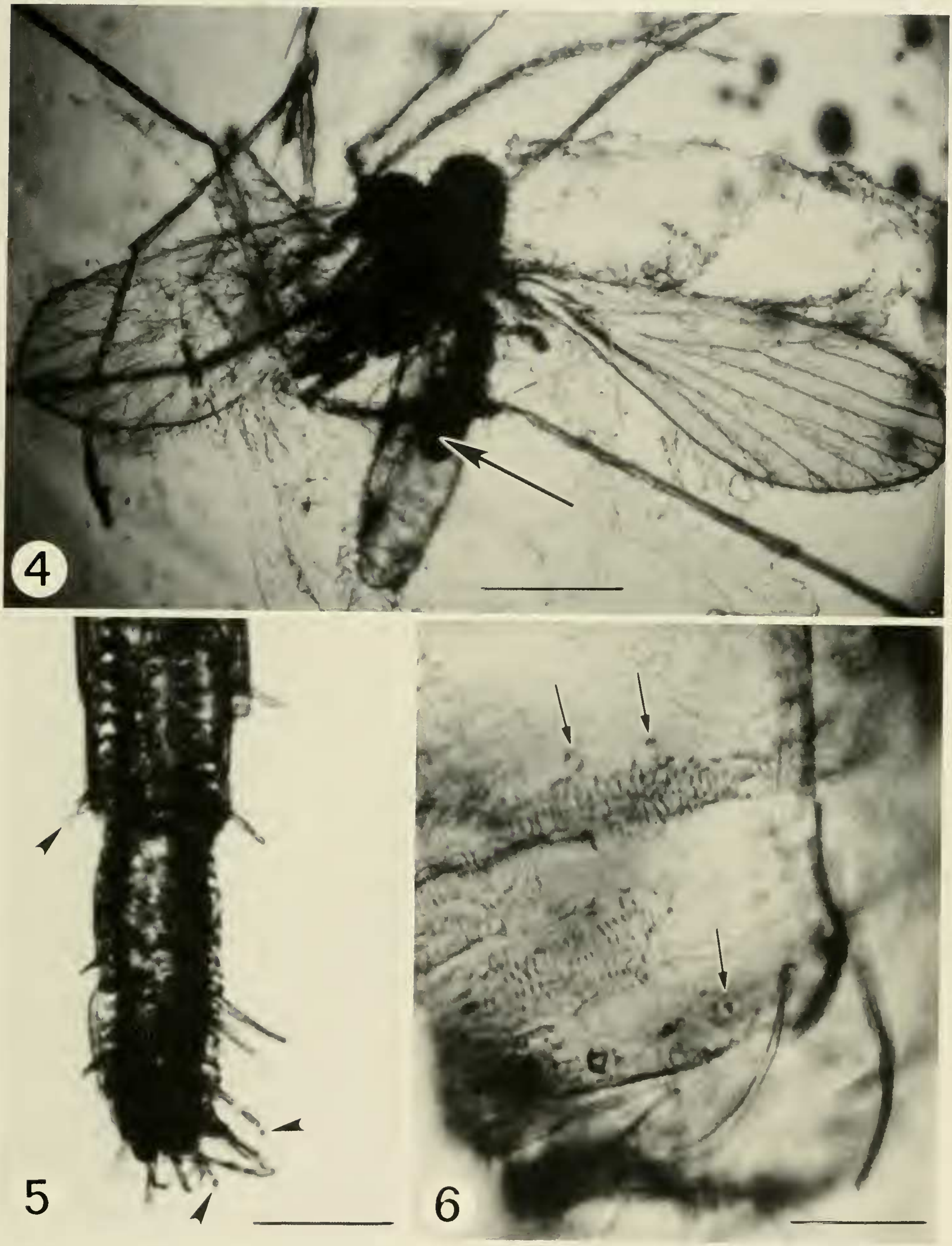
Some similarities also exist between *P. burmitis* and the Lebanese amber *Mesophlebotomites hennigi* Azar et al. (1999). However in that taxon, Sc has a costal branch, Rs is longer than R_{2-4}, R_{2-4} is shorter than R_{2+3}, and R_1 meets the costa in the distal half of the wing. The Lebanese amber *Libanophlebotomus lutfallahi*, Azar et al. (1999) has R_2 perpendicular to the costa, M and CuA_1 joined at the base, and an A_1 vein, all characters which differ from the condition in *P. burmitis*. One similarity between *L. lutfallahi* and *P. burmitis* is the curious venation of Sc/R_1. It is likely that the distal portion of Sc originally made contact with the costa, but then became separated and remained in that condition in some lineages, all of which apparently became extinct during the Cretaceous.

There are also some similarities between *P. burmitis* and the Jurassic *Liassopsychodina pommerana* Ansorge (1994). While the wing venation of *L. pommerana* is unique, especially with the presence of an anal vein, some similarities with *P. burmitis* are a very reduced R_2 in comparison to R_{2+3}, a fairly long R_1, and M_3 and CuA_1 with a similar basal configuration.

Discussion

There are two major extant genera of Old World sand flies, *Phlebotomus* Rondani & Berté and *Sergentomyia* França & Parrot (Lewis 1973). The fossil sand fly possesses some characteristics of members of the genus *Sergentomyia*. One such character is the position of the hairs on the distal ends of abdominal tergites 2 to 6 (Perfilev 1966, Fairchild 1955, Lewis 1973). These are mostly erect in *Phlebotomus* but decumbent in *Sergentomyia*. Only one of these hairs is present in the fossil and it is decumbent. Erect hairs have round sockets while decumbent hairs have elongate sockets (Lewis 1973). In the fossil, the sockets, which are visible, are slightly elongate (Fig. 6). Another *Sergentomyia* character is the short R_2 vein. Early Cretaceous phlebotomids have the R_2 vein shorter than R_{2+3} (Azar et al. 1999), which can be portrayed by the ratio R_2/R_{2+3}, and is under 1.0 in Cretaceous forms. The R_2 vein tends to elongate over time, reaching a ratio of almost 2.0 in modern *Phlebotomus* species (Lewis 1973). Most *Sergentomyia* have retained a relatively short R_2/R_{2+3} ratio (under 1.0), similar to the early Cretaceous forms. A third character linking P. *burmitis* to the genus *Sergentomyia* is the size of the palpal segments. While the fourth palpal segment is usually the shortest in members of the genus *Phlebotomus*, most species of *Sergentomyia* have the second palpal segment smaller (Fairchild 1955), which is the condition in the fossil fly. These morphological characters suggest that *P. burmitis* is a progenitor of the reptile feeding *Sergentomyia* clade. By the Eocene, modern appearing *Sergentomyia* were present (Stuckenberg 1975).

The mouthparts on the fossil are similar to the piercing and sucking forms of extant sand flies (Croset 1969). The presence of elongated stylet-shaped mandibles and maxillae enclosed in an elongate proboscis is an indication that *P. burmitis* possessed the ability to penetrate the skin and take up blood or semi-fluid tissues. However, as stated by Lukashevich and Mostovski (2003) in their review of hematophagous insects in the fossil record, feeding structures are insufficient to determine a definite hematophagous habit without further analysis of gut contents, etc. However, a dark area in the anterior portion of the gut of *P. burmitis* appears to be a recently acquired blood meal. This blood meal extends through the first three abdominal segments and into a small portion of the fourth. According to the stages of blood digestion in



Figs. 4–6. *Palaeomyia burmitis* in Burmese amber. 4, Habitus of fly in amber. Dark area in gut (arrow) shows blood meal. Bar = 0.148 mm. 5, Detail of terminal tarsal segment, showing secretions at tips of some of the setae (arrowheads). Bar = 52 μm. 6, Terminal abdominal tergites showing single decumbent hair and elongate hair sockets (arrows). Bar = 52 μm.

Phlebotomus papatasi Scopoli, Dolmatova (1942) found that just after feeding, vertebrate blood filled the anterior portion of the abdomen up to the last two to three abdominal segments. As digestion proceeded, the blood volume was reduced and after 3–4 hours, the last three to four abdominal segments were cleared of blood. Assuming a similar pattern in *P. burmitis,* it would imply that the ancient sand fly was in the early stages of blood digestion when it became entrapped. While present-day host records of Asian sand flies include both mammals and reptiles (Lewis 1978), since *P. burmitis* was probably a progenitor of the *Sergentomyia* clade, the blood could have come from a reptile. In the midgut of *P. burmitis* are also some microorganisms, which will be the subject of a separate study.

While biting mouthparts can be traced back to the early history of the Diptera and are considered a basic feature in most of the major lineages of that group, actual evidence of blood acquisition in fossil flies has not been previously reported. Downs (1970) speculated that *Phletobomus*-like flies might have represented the earliest forms of Diptera adapted to cut through vertebrate skin and imbibe fluid. The present study confirms blood sucking in early Cretaceous phlebotomids.

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